Accepted Manuscript

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PII: S0016-6995(16)30129-2
DOI: https://doi.org/doi:10.1016/j.geobios.2017.09.002
Reference: GEOBIO 794

To appear in: *Geobios*

Received date: 23-12-2016
Accepted date: 29-9-2017

Please cite this article as: Uchman, A., Quintino, V., Rodrigues, A.M., Johnson, M.E., Melo, C., Cordeiro, R., Ramalho, R.S., Ávila, S.P.,The trace fossil *Diopatrichnus santamariensis* nov. isp. ndash a shell armored tube from Pliocene sediments of Santa Maria Island, Azores (NE Atlantic Ocean), *Geobios* (2017), https://doi.org/10.1016/j.geobios.2017.09.002

The trace fossil *Diopatrichnus santamariensis* nov. isp. – a shell armored tube from Pliocene sediments of Santa Maria Island, Azores (NE Atlantic Ocean) ✡

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[☆] Corresponding editor: Emmanuel Fara.

Abstract

Diopatrichnus santamariensis nov. isp. from lower Pliocene sediments on Santa Maria Island in the Azores Archipelago (mid-North Atlantic) represents the third ichnospecies of *Diopatrichnus* Kern, as characterized by a vertical or inclined tube armoured mainly by bivalve shells that are mostly perpendicular to the burrow axis and concave-upward. The polychaete *Owenia* (family Oweniidae) is favoured as its potential tracemaker based on recent analogues, as opposed to the alternative polychaete *Diopatra* (family Onuphidae). The tracemaker was able to cross oceanic depths, distances, and colonize mid-ocean island sediments. In general, including this example from Santa Maria Island, *Diopatrichnus* occurs mostly within the *Skolithos* and the *Cruziana* ichnofacies.

Keywords:
Ichnology
Ichnotaxonomy
Oceanic islands
Shallow-marine clastics
Polychaetes
Santa Maria Island
Azores

1. Introduction

Some tubiculous marine worms are known to use bioclasts to decorate or strengthen their tubes. The bioclasts may be more or less strictly selected and arranged in a characteristic way, allowing recognition of the tracemaker and differentiation of fossil burrows at the ichnogenus level. A few trace fossils of this type are distinguished on the basis of the

bioclasts, as for example *Lepidenteron* Frič, 1878 (horizontal or oblique tubes lined with fish scales and bones or plant detritus; Suhr, 1988; Jurkowska and Uchman, 2013); *Diopatrichnus* Kern, 1978 (lined with mollusc shells; discussed in this paper); *Crininicaminus* Ettensohn, 1981 (lined with crinoids; Seike et al., 2014); *Nummipera* Hölder, 1989 (mostly vertical tubes lined with Nummulitoidea tests; Jach et al., 2012); *Baronichnus* Breton, 2002 (lined with bryozoan zoaria); *Ereipichnus* Monaco et al., 2005 (horizontal burrows lined with orbitolinid tests and other flat bioclasts), and other unnamed forms (e.g., Papp, 1941).

Some of these ichnogenera are known only from a few occurrences and their possible tracemakers remain poorly identified. Among them, *Diopatrichnus* is known only from the USA, Japan, France, and England, in sedimentary rocks ranging from the Jurassic to the Pleistocene. Its tracemaker was closely allied to the polychaete *Diopatra* Audouin et Milne Edwards, 1833 (Onuphidae) by Kern (1978) and Bromley (1996). Gibert (1996) considered annelids within the families Onuphidae, Owenidae and Terebellidae as the potential tracemakers of *Diopatrichnus oldingi* Gibert, but invoked *Diopatra cuprea* (Bosc, 1802) as the most probable tracemaker. On that ground, the objectives of this paper are: *i*) to present a new ichnospecies of *Diopatrichnus* from Pliocene sediments on Santa Maria Island in the Azores; *ii*) to compare its morphological characteristics with the two already known ichnospecies of *Diopatrichnus*, viz. *D. roederensis* and *D. oldingi*; and *iii*) to review the current knowledge regarding this ichnogenus.

2. Geological setting

2.1. Azores Archipelago

The Azores Archipelago (NE Atlantic Ocean) comprises nine volcanic oceanic islands and a few islets situated *ca*. 1,370 km from mainland Portugal, in an area where the North American, Euroasian and Nubian plates meet at the so-called Azores Triple Junction (Laughton and Whitmarsh, 1974; Fig. 1(A)). The islands rise from a bathymetric anomaly defined by the 2000-m isobath, named the Azores Plateau (Needham and Francheteau, 1974). Santa Maria is the oldest island in the archipelago (*ca*. 6 Ma; Ramalho et al., in press), and the only one with diversified and abundant marine fossils from lower Pliocene (Zbyszewski and Ferreira, 1962; Janssen et al., 2008; Kroh et al., 2008; Winkelmann et al., 2010; Madeira et al., 2011; Meireles et al., 2012; Rebelo et al., 2014, in press; Ávila et al., 2015a, 2015b, 2016; Santos et al., 2015; Uchman et al., 2016) and Pleistocene strata (Ávila et al., 2015c; Ramalho et al., in press).

2.2. Santa Maria Island

Santa Maria has a complex and dynamic geological history, a detailed description of which is given by Ramalho et al. (in press). At *ca*. 6 Ma, the island emerged as a result of surtseyan activity followed by strombolian activity, represented by the Cabrestantes Fm. and Porto Fm., respectively. Thereafter, a broad shield volcano formed from 5.8 to 5.3 Ma, corresponding to the Anjos Volcanic Complex, thus consolidating the island edifice. A marked subsidence trend of *ca*. 100 m.myr^{-1} affected the island probably from the very beginning, and lasted until *ca*. 3.5 Ma. An erosional stage followed the shield volcano stage and during this time interval (from 5.3 to 4.1 Ma), with the first island of Santa Maria being completely razed, creating a large guyot where sediments and organism remains accumulated, intercalated with sporadic, low-volume submarine volcanism (the Touril Volcano-sedimentary Complex). The large majority of the deposits with somatofossils and ichnofossils of Pliocene age were formed during this period (e.g., Malbusca, Pedra-que-pica; Ávila et al., 2015a; Uchman et al., 2016; Rebelo et al., in press). The second island of Santa Maria re-emerged at *ca*. 4.1 Ma, when rejuvenated volcanism (corresponding to the Pico Alto Volcanic Complex) was able to outpace subsidence and breach sea level once again. During this stage, coastlines advanced through the sustained (but intermittent) growth of coastal lava deltas, which completely covered the existing shelf on the eastern side of the island. It was during this stage that the sequence at Ponta do Cedro (Fig. 1(B)) was formed, comprising two overlapping lava deltas separated by wedges of sediments. This volcanic stage lasted until 3.5 Ma, when the subsidence trend reverted to an uplift trend of *ca*. 60 m.myr^{1} that extended to the present times, related to a change from predominantly extrusive to predominantly intrusive edifice growth associated with crustal thickening (Ramalho et al., in press). As a result, a series of 10 marine terraces between 7 and 11 m and 200-230 m above MSL was formed, all located on the windward side of the island. Sporadic volcanism continued until ca. 2.8 Ma, with erosion becoming predominant since then.

2.3. Malbusca section

Malbusca W and Malbusca E outcrops are lodged between two submarine lava-flow sequences that are now exposed along the southern cliffs of Santa Maria (Fig. 1(B, C)). They are different sections of the same laterally continuous layer of highly fossiliferous sediments belonging to the Touril Complex which were dated by Sibrant et al. (2015) with ages ranging from 4.32 ± 0.06 to 4.02 ± 0.06 Ma, the latter in agreement with the age of 4.08 ± 0.07 Ma determined by Ramalho et al. (in press) for the top of the submarine sequence. These

sediments contain abundant invertebrate remains, with molluscs (mostly bivalves) being the most diverse and abundant group, and minor amounts of echinoderms (Madeira et al., 2011), bryozoans, crustaceans (balanids; Winkelmann et al., 2010) and ostracods (Meireles et al., 2012), brachiopods, annelids and corals, as well as some vertebrate shark teeth (Ávila et al., 2015b). Rhodoliths are dominant elements in some facies (Fig. 1(C)); their coralline algae species and palaeoecology were described by Rebelo et al. (2014, in press).

Malbusca W, accessible by sea and from the top of the cliff, has a lateral extension of *ca*. 60 m and the marine sediments have a vertical extension of *ca*. 12 m (facies 3–5; Fig. 1(C)). Malbusca E is best accessed by sea at Ponta da Malbusca and has a lateral extension of *ca*. 400 m and a vertical extension of marine sediments of *ca*. 20 m (facies 2–6; Fig. 1(C)). In both sections, pillow lavas (facies 1; Fig. 1(C)) belonging to the Touril Complex are overlain by a rhodolith rudstone (facies 3 of Malbusca W, facies 2–4 of Malbusca E; Rebelo et al., 2014, in press), which in turn is covered by a shell rudstone 0.6 to 1.2 m thick (facies 5 of Malbusca E; Fig. 1(C)). Thick cross-bedded sands (facies 4 of Malbusca W; facies 6 of Malbusca E), which change into highly bioturbated sands (facies 5 of Malbusca W; Fig. 1(C)) cap the rhodolith and shell rudstones, concluding the sedimentary sequence, except at Malbusca E, where they are truncated eastward and overlain by sandstones with hummocky and swaley cross-stratification, before being capped overall by a submarine lava flow sequence. The bioturbated sands contain several trace fossils, the most common being *Macaronichnus segregatis* Clifton et Thompson, 1978. Other ichnofossils reported by Uchman et al. (2016) from these outcrops are *Piscichnus*, *Thalassinoides*, *Asterosoma*, *Bichordites*, *Palaeophycus*, ?*Parmaichnus*, ?*Psilonichnus*, and *Ophiomorpha*. *Diopatrichnus* isp. was found in poorly sorted, medium-grained calcareous arenites (Malbusca W) and in poorly sorted, medium to coarse-grained calcareous lithic arenites with shells (Malbusca E).

2.4. Ponta do Cedro section

The Ponta do Cedro section is located on the island's eastern coast (Fig. 1(B, C)). Its calcareous sedimentary rocks were exploited for lime production and exported to the other Azorean islands during the 18th and 19th centuries (Madeira et al., 2007). The sediments at Ponta do Cedro consist of two wedges (wedge 2 over wedge 1; facies 2 and 3; Fig. 1(C)), with a maximum lateral extension of *ca*. 65 m, which are nested against the slope of a lava delta and are draped partly by a layer of pyroclastic sand. The wedges are capped by pillow-lava basalt (facies 4; Fig. 1(C)) of a later lava delta, dipping to the eastern quadrant. The lava delta slope and its foresets dip to the east at an angle of 34–36°. The more or less flat top of the

delta is located at an altitude of *ca*. 58–60 m a.s.l. At Ponta do Cedro, *Diopatrichnus* isp. was found in poorly sorted, medium-grained calcareous arenites.

3. Systematic paleoichnology

Ichnogenus ***Diopatrichnus*** Kern, 1978

Type ichnospecies: *Diopatrichnus roederensis* Kern, 1978 from the Mission Valley Fm. (middle Eocene) of California, USA.

Emended diagnosis: A cylindrical, mostly vertical to inclined tube, thickly lined mainly with mollusc shell valves or their fragments, additionally with other bioclasts or lithic components, which altogether are oriented mostly perpendicularly or obliquely to the tube axis.

Remarks: Kern (1978: p. 187) provided a diagnosis of *Diopatrichnus* as follows: "*Diopatrichnus* is a cylindrical tube, lined largely with shells of bivalve molluscs but also with other molluscs, plant fragments, and other dominantly platy materials. These lining materials are attached to the tube at their edges, and their free edges are inclined upward and outward and overlap one another in an imbricate manner. The tubes are essentially straight, though they may have a short inclined segment at the upper end, and they generally are oriented between 60° and 90° to the plane of stratification". This diagnosis refers to *D. roederensis,* which was the first described ichnospecies of *Diopatrichnus*. The description details do not entirely cover the morphology of *Diopatrichnus oldingi* Gibert, 1996, described later, and the *Diopatrichnus* from Santa Maria presented in this work. For instance, the imbrication mentioned by Kern (1978) does not occur in these ichnotaxa. Moreover, the original diagnosis contains an interpretation of the tracemaker. Therefore, it was emended as above.

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Figs. 2–4

Derivation of the name: From Santa Maria Island, where this trace fossil occurs.

Holotype: Specimen INGUJ240P1 (Fig. 2), housed in the Geological Museum of the Jagiellonian University, Kraków.

Type locality and horizon: Ponta do Cedro section, Santa Maria Island, Azores; Touril Volcano-sedimentary Complex (Pliocene).

Other material: Six uncollected, well preserved and documented fossil burrows (Figs. 3, 4). A small fragment of burrow D was also collected for thin section analysis.

Diagnosis: *Diopatrichnus* in which the bivalve shell valves or their fragments are mostly concave-upward.

Description: The holotype, specimen INGUJ249P1 (Fig. 2), is a 10 cm-long collected part of a straight vertical tube observed in the field in the Ponta do Cedro section, at the top of wedge 1. The tube is at least 25.5 cm long. Its upper part was incomplete because of recent erosion and the lowest part plunges into the rock. The external diameter of the tube ranges from 25 to 30 mm and its lumen is 11–15 mm in diameter. Its thick wall is composed of small, mostly crushed bivalve shells (in fact shell valves or their fragments), perpendicular to the burrow axis, most of them oriented convex-upward. Some of the shells are slightly bioeroded with *Entobia* isp. and encrusted with bryozoans. The lumen margin lacks any smoothing or internal layer (this can be either a primary feature or the result of decomposition of organic parts). It is more even than the outer margin of the burrow, which is jagged because of shells sticking out. The lumen and the space between shells are filled with volcaniclastic sandstone, which is the same as in the surrounding rock. In the holotype (Fig. 2), the shells are more loosely packed and more variably inclined with respect to the burrow axis, as compared to burrows A, D, and E (Figs. 3, 4; see below).

In burrow A (west fault of Malbusca section), the tube is straight, slightly inclined under the angle of 80°, 48 cm long, with an external diameter of 42–48 mm (Fig. 3(A, B)). Its lumen is 15–18 mm in diameter. The lining consists almost exclusively of small bivalve shells including pectinids. Sandstone similar to that from the surrounding strata fills the space between the shells. The shells are arranged mostly perpendicular (and horizontally) to the tube and concave-upward. The external margin of the lining is very uneven; the internal margin is more even, but without any smoothing or internal layer. Both terminations of the tube are diffuse.

In burrow B (Malbusca E section), the tube is *ca*. 30 cm long (Fig. 3(C, D)). Its lower-middle part (24 cm) is almost vertical. The upper part is bent down to follow initially a slightly inverted course and then changes obliquely upward at the end. The external diameter of the tube is 24–27 mm. The lumen is 10–12 mm in diameter. The lining consists almost exclusively of crushed, thin bivalve shells including pectinids. A few barnacle scuti were found, as well as remains of spines of the sea-urchin *Eucidaris tribuloides* (Lamarck, 1816). The shells are partly bioeroded with the clionaid sponge boring *Entobia* isp.; some are encrusted with bryozoans. The shells are mostly randomly arranged and positioned mainly normally or obliquely to the tube. The external surface of the tube is rough. Its terminations are diffuse at both ends.

In burrow C (Malbusca E section), the tube is 22 cm long and inclined at a 60° angle to the bedding (Fig. 3(E)). The external diameter is 20 mm and the lumen is 10 mm in diameter. The lining and terminations are as described for specimen B.

Burrow D (Ponta do Cedro section) lies in a large fallen block of thickly layered lithic calcareous arenite, which probably derives from wedge 2. The tube is straight, perpendicular to the layering of the bedding, at least 30 cm long, and maximally 48–65 mm in diameter (Fig. 4(A, B)). The lumen is 10–11 mm in diameter. The lining is composed of flat or slightly concave fragments of shells, which are perpendicular to the lumen, parallel to the layering, and concave-upward, with a high contribution of sand grains, distinctly higher than in burrow A (Fig. 4(B)). Moreover, a few single bryozoans and small, elongate basaltic pebbles and sand grains are incorporated in the lining. Some of the shells are bioeroded with the sponge boring *Entobia* isp. Some spaces between the shells and sand grains are filled by calcite cement (Fig. 4(C)). The upper part of the tube passes into an indistinct curved, oblique tube (?) marked by subtle lithological changes (better cementation and packing of grains) but without any bioclastic lining and expressed in the weathering relief.

Burrow E (Ponta do Cedro section, wedge 2) is a short vertical tube, 10.5 cm long, maximally 50 mm wide, with lumen 17 mm in diameter (Fig. 4(D)). The lining is composed of flat or slightly concave fragments of shells, perpendicular to the lumen and concave-downward. Moreover, small, single lithoclasts are present. The termination is diffuse.

Burrow F (Ponta do Cedro section, wedge 2) is a short oblique tube, inclined at 45° (Fig. 4(E)). The tube is 8.3 cm long. The external diameter and the lumen diameter are 20 and 12 mm, respectively. The lining is very thin and composed of sparsely distributed bioclasts of bivalve shells adhering to the lumen. The upper and lower terminations are sharp and perpendicular to the lumen.

Remarks: Burrow A (Fig. 3(A, B)) is probably the longest *Diopatrichnus* structure ever found. Terminations of burrow E (Fig. 4(D)) may be incomplete due to erosion or decomposition of organic matrix binding the bioclasts in part of the tube. The burrows occur in a massive and very hard rock. Mechanical cutting of specimens or their parts, although possible, is difficult due to logistic and formal constraints associated with protected area regulations of the PalaeoPark Santa Maria. Therefore, the burrow was left in the field.

4. Discussion

4.1. Ichnospecies affinity

Until now, two ichnospecies of *Diopatrichnus* have been described: *D. roederensis* Kern, 1978 and *D. oldingi* Gibert, 1996. *Diopatrichnus oldingi* (Bathonian of England) is small, 20–40 mm long, 1.5–5 mm in diameter, with lining 0.25–1.8 mm thick, composed of imbricated bivalve and gastropod shell fragments, peloids and ooids. *Diopatrichnus roederensis,* which is known from fine sandy mudstones of the late middle or early late Eocene Mission Valley Fm. (California, USA), is larger. The tube is vertical or oblique, up to 25 cm long, with lumen diameter in the range of 11–23 mm. Its lining is composed of shell fragments but also contains plant debris. All specimens from Santa Maria are in the size range of *D. roederensis* or larger. The most important difference between *D. roederensis* and *D. santamariensis* nov. isp. concerns the arrangement of shells in the lining. In *D. roederensis,* shells are mostly concave-down, and commonly inclined toward the lumen. In the holotype of *D. santamariensis* nov. isp. and in burrows A, D, and E, shells are mostly perpendicular and mostly concave-up. In the holotype and in burrows B and C, the lining shells are less orderly than in burrows A and D, but in burrow E, the order changes along the tube (Fig. 3(D)). The order lines of arrangement of shells in the burrows is rather within the intraspecific variability, not a potential ichnotaxobase (i.e., it should not constitute a criterion for ichnotaxonomic differentiation). Specimen F (Fig. 4(E)) differs from all the other discussed specimens, but is interpreted as a reworked tube that lost its original morphology (see below).

4.2. Ethological interpretation of morphology and tracemaker affinity

The vertical or steeply inclined orientation of *Diopatrichnus santamariensis* nov. isp. with a curved segment (burrows B, D) can be referred to a burrow lining embedded in the sediment and partly to chimneys (tube caps) that extend out of the sediment. However, as recent polychaete tubes exhibit, the proportions between parts hidden in the sediment and sticking above can be different. In Ria de Aveiro (north of mainland Portugal), the *Diopatra neapolitana* tube can stick out for 2–4 cm above the sediment, but extend more than 70 cm into it, depending on the size of the worm, whereas the *Owenia fusiformis* tube can be almost concealed within the sediment (Victor Quintino and Ana M. Rodrigues, pers. obs.). In Tom's Cove (Virginia, USA), *Diopatra cuprea* reaches a size of 30 cm long, with a tube length of 1 m and a tube cap of 5 cm (Woodin, 1978). The subsurface part of the burrow and the cap are herein referred to as a tube. The lower to middle part of the tube in burrow B is a burrow in the sediment, while its curved upper part may be the tube cap (Fig. 3(C)). Similarly, the indistinct, curved prolongation of the tube in burrow D (Fig. 4(A)) can also be a tube cap, but devoid of bioclastic lining. The bioclastic lining in this part of the tube could have been

destroyed, or this part of the tube only displayed the organic lining, similar to the lower part of the *Diopatra* tube in Fig. 5(A, B)). In burrows A, C, and E, the cap was probably detached and only the tube embedded in the sediment was preserved. Burrow F may represent a detached cap, whose bioclastic lining was partly peeled off by currents. Its sharp terminations and oblique arrangement suggest that it is a sort of bioclast entrained in the sediment. Similarly, at least part of specimens of *Diopatrichnus oldingi* are interpreted as detached, allochthonous tube caps (Gibert, 1996).

The 40 cm-long burrow A is especially intriguing because of its extraordinary length. *Diopatra cuprea* regulates length of the cap by rebuilding or detachment depending on accumulation or erosion; a new cap can be pulled down through newly deposited sediments in order to join to the older, armoured tube (Myers, 1970, 1972; Bromley, 1996). The ability for such down-pulling activity is rather limited, so it seems that the very long armoured tubes reflect rather low rates of sediment accretion. It seems that the long tube of burrow A was built during accumulation of the sediment throughout the maker's life. This shows that almost 50 cm of sediment was deposited during the life of the tracemaker. An alternative explanation would be that the animal was a long one and so was the tube. It is known that *Diopatra neapolitana* Delle Chiaje, 1841, can be as long as 60–70 cm and builds longer tubes (Rodrigues et al., 2009; Pires et al., 2012).

So far, *Diopatra* Audouin et Milne Edwards, 1833 (Onuphidae) has been considered as the recent equivalent of the tracemaker of *Diopatrichnus* (Kern; 1978; Bromley, 1996). Gibert (1996) similarly indicated *Diopatra cuprea* (Bosc, 1802) as the most probable tracemaker annelid of *Diopatrichnus oldingi* Gibert, but he also considered the families Owenidae and Terebellidae. *Diopatra cuprea* is known from warm and temperate shelf seas. It reinforces the anterior part of the tube, off the bottom, using variable bioclasts glued by mucus. The function of tube caps is variable and considered as food traps, camouflage, barrier for sediment inflow into the burrow, and a tool in water exchange (Skoog et al., 1994). The reinforced tube and cap can be buried by sediment and a new cap above can be rebuilt (Myers, 1970, 1972). *Diopatra* species have worldwide distribution and exist in water depths ranging from the intertidal zone up to over 500 m (*fide* Encyclopaedia of Life, www.eol.org).

Krejci-Graf (1936) observed recent *Diopatra*-like tubes lined with shells in southern China coastal areas, the lower part of which was in sand while the upper, flexible part bent over the sand surface. The tubes were *ca*. 1 cm in external diameter. Richter (1928: pl. 3, fig. 1) reported tubes of the polychaete *Lanice* (family Terebellidae) lined with sand grains and shells from the North Sea. *Lanice conchilega* (Pallas) is mostly sand-lined but can contain

shells of molluscs and other bioclasts, especially in its upper part (Ziegelmeier, 1952; Callway, 2003).

Diopatrichnus is more similar to the tube of *Owenia* than to the tube of *Diopatra* or *Lanice.* Oweniids comprise a small taxon and live in tightly fitting tubes (Rouse and Pleijel, 2001). Adults lengths range usually from 10 to above 100 mm, but the tubes of larger worms of *Owenia fusiformis* can reach up to 300 mm (Rouse and Pleijel, 2001). *Owenia fusiformis* Delle Chiaje, 1844 is a typical soft-bottom species, found preferentially in muddy sand/sandy sediments; it is usually 3–10 cm long, 2–3 mm wide, and has a life span from 3 to 4 years (Fauvel, 1927; Ménard et al., 1990). The tubes are made up by shell fragments, occasionally including sand grains or calcareous fragments, imbricated like roof tiles and stuck tightly by mucus (Dauvin and Thiébaut, 1994). They contain also sand grains, preferentially composed of heavy minerals (Fager, 1964). Although likely to comprise multiple species, *Owenia fusiformis* presents a worldwide distribution, recognized in coastal regions throughout northwest Europe, the Mediterranean, the Indian Ocean, and the Pacific (Dauvin and Thiébaut, 1994). This species is most abundant between 0 and 40 m, but is known to inhabit waters as deep as 2350 m (Dauvin and Thiébaut, 1994; Rouse and Pleijel, 2001).

Owenia seems to be a more suitable tracemaker analogue than *Diopatra*, taking into consideration the biogenic elements and morphology of the tubes of modern species (Table 1). Besides other elements, both use sand grains and shells in their tube construction. The *Diopatra* tube is made up mainly of sand and/or mud particles, with shells (when available in the environment) and other materials including plants, mainly in the cap. The *Owenia* tube can be lined with shells along its full length (Fig. 5(C)), more similar to the case of burrow A in this paper, which is very long (Fig. 3(A)). The arrangement of the shells is also different in the *Diopatra* and *Owenia* tubes. In *Diopatra* the shells are mostly arranged in the tube cap (Fig. 5(A, B)), serving namely as camouflage or to protect the tube entrance (Brenchley, 1976), while in *Owenia* they are a prominent feature of the tube, arranged like roof tiles along its whole length, and take on a structural role (Fig. 5(C). This feature is well seen in burrow A described above (Fig. 3(A, B)). This burrow, however, is much longer than the extant *Owenia* tubes and closer to the length of some *Diopatra*, such as *D. neapolitana*, which attains more than 70 cm in length (Rodrigues et al., 2009) or *D. cuprea*, which tube reaches 1 m (Woodin, 1978). *Owenia* also may have attained longer dimensions in the past and this possibility cannot be excluded. Both *Owenia* and *Diopatra* are found worldwide (Dauvin and Thiébaut, 1994; Jumars et al., 2015) but due to their reproduction and development characteristics, *Owenia* has a higher chance of being transported to new habitats. Indeed, *Diopatra* species

have direct development (without larval stages) or lecithotrophic larvae (dependent on yolk) that feed only after settlement (Blake, 1975; Giangrande, 1997; Pires et al., 2012a, b), and develop into juvenile after 5-6 days (Bhaud and Cazaux 1987, Conti and Massa 1998, Pires et al., 2012). Conversely, *Owenia* produces pelagic planctotrophic larvae that live in the plankton for 11-30 days. Although not dispersed passively by currents, larvae with longer periods in the plankton show higher dispersal distances, as demonstrated by Shanks et al. (2003). The occurrence of *Diopatrichnus* in the mid-Atlantic region agrees with this. Jumars et al. (2015) classified *Owenia* as discretely motile, despite living in a tube. The tube is flexible and can bend over to the sediment surface in deposit feeding in order to emerge from the sediment when it is buried by sediment deposition. In that connection, it is noteworthy that the tube represented in Fig. 3(C) is bent, showing more similarities to a bent *Owenia* tube than to a *Diopatra* tube, but we do not know if the bending is primary or secondary.

4.3. Palaeoenvironmental and stratigraphic range

In the Malbusca E section, *Diopatrichnus santamariensis* nov. isp. occurs in the lower part of the section, *ca*. 1 m above the basalt basement, in poorly sorted, medium to coarse-grained lithic calcareous arenites with shells and sparse sandstone intraclasts. Associated trace fossils include vertically oriented *Macaronichnus segregatis* (Fig. 2(D, E)) accompanied by *Ophiomorpha* isp., ?*Psilonichnus* isp., and *Palaeophycus* isp. (Uchman et al., 2015, 2016). These sediments rest on an uneven cover dominated by rhodoliths covering basalts (Rebelo et al., in press). All these sediments are part of a transgressive sequence deposited above the storm wave-base level; they represent shallow marine environments still under the influence of storms. For a detailed description of the Malbusca E section, see Uchman et al. (2016) and Rebelo et al. (in press).

In the Malbusca W section, *Diopatrichnus santamariensis* nov. isp. (burrow A) was found at the top of the section, to the west of a fault, in a metre-thick bed of poorly sorted, medium to coarse-grained lithic calcareous arenites with dispersed, disarticulated bivalve shells – including, e.g., *Pecten dunkeri* Mayer, *Spondylus* sp., *Mimachlamys varia* (Linnaeus, 1758), *Manupecten pesfelis* (Linnaeus, 1758), *Ostraea* sp., *Arca noae* Linnaeus, 1758, and *Lopha plicatuloides* (Mayer, 1864). Barnacles (*Zullobalanus santamariaensis* Buckeridge et Winkelmann, 2010) and remains of irregular echinoids (spines of *Eucidaris tribuloides* (Lamarck, 1816) and tests of *Clypeaster altus* (Leske, 1778)) are common elements, whereas fragments of shells of the termophilic mollusc gastropod *Persististrombus coronatus* (Defrance, 1827) are rare. Regarding trace fossils, only rare *Macaronichnus segregatis* co-

occurs. The sediments are covered by uneven and lithologically variable pyroclastic sands and coarser sediments (*ca*. 50 cm), followed by submarine basalts. Further to the east of the fault, the arenites rest on finer lithic arenites containing *Macaronichnus segregatis,* mostly vertically oriented *Thalassinoides* isp., *Ophiomorpha* isp., and *Piscichnus* isp. The facies features and the section context suggest a shallow marine environment, similar to Malbusca E. For a detailed description of Malbusca W section, see Uchman et al. (2016).

In Ponta do Cedro, *Diopatrichnus santamariensis* nov. isp. (the holotype and burrows D–F) occurs in a wedge of poorly sorted medium- to coarse-grained lithic calcareous arenites in association with *Thalassinoides*. This sedimentary wedge was deposited over the frontal slope of a lava delta, at a depth of a few tens of metres (unpubl. data).

The ichnogenus *Diopatrichnus* is known to occur in different environments. The depth of the mudstone lens bearing *D. roederensis* in the Eocene of California was estimated as a few to 100 m (Kern, 1978), while the environment of the Bathonian *D. oldingi* from England was determined as "quiet" subtidal (Gibert, 1996). *Diopatrichnus* (lumen 2.9 cm and exterior 4.4 cm in diameter, up to 16 cm long) was reported as abundant at a shallow marine condensed fossiliferous, glauconitic muddy sands of the middle Eocene Lisbon Fm. of southern Alabama, USA, within the *Cruziana* ichnofacies, together with *Thalassinoides*, *Rosselia*, *Asterosoma*, *Teichichnus*, *Planolites*, and *Ophiomorpha* (Urash, 2004). The lining was dominated by small, concave-up, nested bivalve shells, locally with small solitary corals. *Diopatrichnus* (*ca*. 2 cm of external diameter) was also reported in the underlying Eocene Tallahatta Fm. (stratigraphically condensed, fossiliferous muddy sand), together with *Thalassinoides* and *Asterosoma* (Savrda et al., 2005), as well as from fjord-head deposits (Buatois and Mángano, 2011) and in Pleistocene glaciomarine diamictites of the Yakataga Formation in the Gulf of Alaska, together with *Teichichnus*, *Rhizocorallium*, and *Zoophycos* (James et al., 2009). This ichnogenus was also reported from the Miocene (Badenian) of western Ukraine as "tube of a polychaete of *Diopatra*-type" and considered as an "intertidal fossil" (Wysocka et al., 2012), and from middle Pleistocene lower shoreface sediments belonging to the Kongochi Fm. of Japan (Nara, 1998). Tubes up to 12 cm long, with diameter up to 3 cm occur in the open shelf mudstones and sandy mudstones of the Ripley Fm. (Maastrichtian) in Alabama, USA, together with *Chondrites, Phycosiphon*, and *Planolites* (Hall and Savrda, 2008), suggesting a low-energy environment. Phillips et al. (2011) also reported *Diopatrichnus* isp. (1.5–2.0 cm wide) lined with shells in slope to distal ramp mudstones of the Marnes Bleues Fm. (Priabonian–lower Oligocene) in SE France.

The occurrence of *Diopatrichnus* in the Azores Islands shows that the tracemaker could be transported across an open ocean, probably by means of dispersion in the plankton. This possibility better fits *Owenia* than *Diopatra*, because the larval stage of *Owenia* spans up to 30 days in the water column, whereas larvae of *Diopatra* span only 5 to 6 days in the water column. This longer period gives *Owenia* a better chance of being transported through long distances (Shanks et al., 2003).

In summary, the combination of a literature review and current Santa Maria data indicate that *Diopatrichnus* is known from the Bathonian, Maastrichtian, and Eocene–Pleistocene, mostly from shallow-marine environments, from the *Skolithos* and the *Cruziana* ichnofacies (including the distal variety of the latter), and occasionally in deeper (slope) settings, in different climatic zones including cold waters in the Pleistocene. Bromley (1996: p. 249) placed *Diopatrichnus* within his *Arenicolites* ichnofacies, which refers to storm and other event deposits, but this ichnofacies is rarely used (e.g., MacEachern et al., 2012). Almost all occurrences of *Diopatrichnus* suggest that this trace fossil is not abundant, except for the Eocene Lisbon Fm. in Alabama, USA (Urash, 2004). The present study clearly indicates that *Diopatrichnus* can also occur in remote volcanic oceanic island environments isolated by oceanic depths, such as the Azores Archipelago. In contrast to the findings of Gibert (1996), who included the Oweniidae as potential tracemakers of *Diopatrichnus* but concluded that *Diopatra cuprea* was the most likely candidate, this study supports the idea that species of *Owenia* are the most probable tracemakers of *Diopatrichnus*.

5. Conclusions

Diopatrichnus santamariensis from the Neogene (lower Pliocene) shallow-marine sediments of Santa Maria Island in the Azores is a new ichnospecies of *Diopatrichnus*, in addition to the previously known ichnospecies of *D. roederensis* Kern, 1978, and *D. oldingi* Gibert, 1996. It is represented by a vertical to subvertical tube with a thick wall mostly built of bivalve shells, having an orientation perpendicular to the burrow axis and usually lodged in a concave-up position. The tubiculous polychaete *Owenia* is the most probable tracemaker of *Diopatrichnus,* as opposed to *Diopatra,* a still much-favoured candidate. The material studied and the literature review show that *Diopatrichnus* occurs in the *Skolithos* and the *Cruziana* ichnofacies.

Acknowledgements

We thank the Direcção Regional da Ciência, Tecnologia e Comunicações (Regional Government of the Azores), FCT (Fundação para a Ciência e a Tecnologia) of the Portuguese government, and Câmara Municipal de Vila do Porto for financial support, and the Clube Naval de Santa Maria and Câmara Municipal de Vila do Porto for field assistance. We are grateful to the organizers and participants of several editions of the International Workshops "Palaeontology in Atlantic Islands" who helped in fieldwork (2002, 2005-2016). Alfred Uchman received additional support from the Jagiellonian University (DS funds). Carlos Melo is funded by M3.1.a/F/100/2015 by FRCT/Açores 2020 (Fundo Regional para a Ciência e Tecnologia). S. Ávila and R. Ramalho acknowledge their FCT Investigator research contracts (2015) funded by the Portuguese Science Foundation. This work was also supported by FEDER funds through the Operational Programme for Competitiveness Factors - COMPETE and by National Funds through FCT - Foundation for Science and Technology under the UID/BIA/50027/2013 and POCI-01-0145-FEDER-006821. Thanks are also due, for the financial support, to CESAM (UID/AMB/50017/2013), to FCT/MEC through national funds, and the co-funding by the FEDER, within the PT2020 Partnership Agreement and Compete 2020. Andrew K. Rindsberg and an anonymous reviewer improved the text and provided helpful comments.

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Table and Figure captions

Table 1. *Diopatra* and *Owenia* main characteristics

Fig. 1. Location maps and stratigraphic columns. **A**. Location of the Azores archipelago in the NE Atlantic, and geotectonic setting of Santa Maria Island within the Azores triple junction. MAR: Mid-Atlantic Ridge; EAFZ: East Azores fault zone. **B**. Location of the outcrops where *Diopatrichnus santamariensis* nov. isp. was found. **C**. Stratigraphic columns of Malbusca W, Malbusca E, and Ponta do Cedro.

Fig. 2. Holotype of *Diopatrichnus santamariensis* nov. isp. from Ponta do Cedro (lower Pliocene; Santa Maria Island, Azores). **A**. View of the burrow in the field, which upper part was collected. **B**. The holotype (upper part of the burrow in A), INGUJ240P1. **C**. View of the holotype from the top. Scale bars: 3 cm (A), 1 cm (B, C).

Fig. 3. *Diopatrichnus santamariensis* nov. isp. from Malbusca (lower Pliocene; Santa Maria Island, Azores). **A**. Burrow A, general view, Malbusca W. **B**. Detail of A. **C**. Burrow B, general view, Malbusca E. **D**. Detail of C, with *Macaronichnus segregatis* (*Ma*) and a crustacean burrow (cb). **E**. Burrow C, Malbusca E. Scale bars: 10 cm (A), 3 cm (B–E).

Fig. 4. *Diopatrichnus santamariensis* nov. isp. from Ponta do Cedro (lower Pliocene; Santa Maria Island, Azores). **A**. Burrow D in lithic arenites with basalt pebbles (bp). **B**. Detail of A; note the lithic elements included in the lining. **C**. Thin section crossing vertically a fragment of lining in burrow D. **D**. Burrow E. **E**. Burrow F. Scale bars: 10 cm (A), 1 cm (B), 5 mm (C), 3 cm (D, E).

Fig. 5. Tubes of recent *Diopatra neapolitana* (**A, B**) and *Owenia fusiformis* (**C**), from the intertidal zone of Ria de Aveiro, Portugal (A, B) and shelf fine sand bottom off the Tagus Estuary, Lisbon, Portugal, from *ca*. 40 m water depth (C). The *O. fusiformis* tube (C) derives from the photographic exhibition by one of us (VQ) “Revelations: life in the sand, life in the rocks”; it is only approximately to scale. Scale bars: 1 cm (A, B), *ca*. 5 mm (C).

Table 1.

Characteristics	***Diopatra***	***Owenia***
Word distribution	worldwide distribution (several species)	worldwide distribution
Max. length of worm and tube	70 cm and > 100 cm	10 cm and 30 cm
Tube characteristics	flexible with cap projecting up to 5–10 cm above the sediment	flexible with the anterior end projecting above the sediment (1–2 mm); without a cap like in *Diopatra*
Tube elements arrangement	sand/mud grains, shells or plant debris, randomly arranged on the tube cap	sand grains, shell fragments along its full length, overlapping
Development	direct; lecithotrophic larvae (5–6 days in the water column)	planctotrophic larvae (11–30 days in the water column)
Feeding method	predators; omnivorous	Active suspension feeder, Surface deposit feeder